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Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (*Puffinus griseus*)

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ABSTRACT

Non-breeding sooty shearwaters are the most abundant seabird in the California Current Large Marine Ecosystem (CCLME) during boreal spring and summer months. This, combined with relatively great energy demands, reliance on patchy, shoaling prey (krill, squid, and forage fishes), and unconstrained mobility free from central-place-foraging demands—make shearwaters useful indicators of ecosystem variability. During 2008 and 2009, we used satellite telemetry to evaluate shearwater ranging patterns throughout the CCLME and specifically within the US Exclusive Economic Zone (EEZ) among birds captured at three locations: Columbia River Plume, WA; Monterey Bay, CA; and Santa Barbara Channel, CA. Shearwaters ranged throughout the entire CCLME from southeast Alaska to southern Baja California, Mexico. Within the EEZ during 2008 and 2009, shearwaters spent 68% and 46% of time over the shelf (<200 m), 27% and 43% of time over the slope (200–1000 m), and 5% and 11% of time over the continental rise and abyssal regions (>1000 m), respectively. In 2008 and 2009, shearwaters spent 22% and 25% of their time in the EEZ within the five west coast National Marine Sanctuaries, respectively; high utilization occurred in non-sanctuary waters of the EEZ. Shearwater utilization distribution (based on the Brownian-bridge movement model) among sanctuaries was disproportionate according to sanctuary availability (based on area) within the EEZ. Shearwaters utilized the Monterey Bay sanctuary (2008, 2009) and the Channel Islands sanctuary (2009) disproportionately more than other sanctuaries. Although all five sanctuaries were used by shearwaters, waters outside sanctuary zones appeared significantly more important and likely supported large aggregations of shearwaters. Utilization distributions among individual birds from three discrete capture locations were variable and revealed greater similarity in space-use sharing within capture-location groupings and during 2008 when shearwaters were more aggregated than in 2009. We identified several regional “habitat hotspot” areas, including the Columbia River Plume, Cape Blanco, Monterey Bay, Estero/San Luis Obispo Bays, and the eastern Santa Barbara Channel through the inner Southern California Bight.

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1. Introduction

“As the most visible of all marine organisms, and as strong indicators of physical oceanographic attributes and the distribution and abundance of lower trophic level species, understanding seabird concentrations and aggregations at sea provides a rich information base from which marine protected areas can be designed” (Lascelles, Ronconi, Langham, this issue)

Seabirds are excellent indicators of marine ecosystems (Piatt et al., 2007; Einoder, 2009). As such, we posit sooty shearwaters (*Puffinus griseus*, Family Procellariidae) to be valuable indicators of ecosystem productivity and structure at two scales: regional (California Current Large Marine Ecosystem [CCLME]), and local (embayments, water masses contained within west coast US National Marine Sanctuaries). For example, with an estimated population numbering between 20–30 million individuals, sooty shearwater is one of Earth's most numerous seabirds (Newman et al., 2009), yet large declines in abundance (Veit et al., 1997; Scott et al., 2008) have prompted the ICUN to list the species as “Near Threatened” (BirdLife International, 2010). Annually during April–May, the majority of the sooty shearwater population migrates to the northern hemisphere. Year-round tracking from

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New Zealand using coarse-scale geolocation technology (Burger and Shaffer, 2008) revealed shearwaters use one of three well-defined northern hemisphere 'wintering areas': the western North Pacific off Japan and Russia, the central-northern Gulf of Alaska, and the California Current region (Spear and Ainley, 1999; Shaffer et al., 2006). Within these three areas, sooty shearwaters are major components of the avian community (Briggs et al., 1987; Wahl et al., 1989; Springer et al., 1999). During April through September, non-breeding sooty shearwaters numerically dominate the CCLME marine avifauna (ca. 60% of the total number of seabirds observed at sea; Briggs et al., 1987; Ainley et al., 1995; Oedekoven et al., 2001; Hyrenbach and Veit, 2003; Ainley and Hyrenbach, 2010). For instance, using data presented by Shaffer et al. (2006), if we estimate one-third of the New Zealand breeding population (ca. 21.3 million, Newman et al., 2009) wintered (austral) in the CCLME, this would equate to approximately 7 million individuals (not including birds from Chilean colonies for which there are few reliable population estimates; but see Reyes-Arriagada et al., 2007). This is similar to the 4.9–6.9 million individuals estimated by summing previous CCLME estimates during peak abundance (i.e., approximately May–July; 2.2 million off Oregon Weins and Scott, 1975 and 2.7–4.7 million off California Briggs et al., 1987). Shearwaters tend to travel *en masse* with single flocks numbering greater than 100,000s birds and extended across many square kilometers (Briggs et al., 1987). Furthermore, shearwaters exhibit great mobility, unconstrained by the need to return to a breeding colony. As wing-propelled divers, shearwaters can reach >60-m depth (Shaffer et al., 2009) and thus can integrate foraging conditions (e.g., availability of certain prey) throughout the ocean's upper mixed layer. Because shearwaters have the capacity for rapid and extensive redistribution to areas with enhanced prey availability, beyond the temporal and spatial scale of ship-based surveys, tracked shearwater movements can be used to understand how the overall population disperses throughout the CCLME as individuals respond quickly to rapid (hours to days) environmental changes in oceanic conditions such as upwelling and relaxation events and dynamic frontal boundaries (Briggs and Chu, 1986; Ainley et al., 2009). In turn, telemetry information can be used to delineate important marine regions where forage fish resources and trophic transfer of energy are expected to be high.

The US National Marine Sanctuaries Act (1972) was established to recognize and help protect important marine areas within the United States Exclusive Economic Zone (i.e., waters from the US coastline to 200 NM offshore; US EEZ). During 1980 to 1994, five National Marine Sanctuaries (hereafter, sanctuaries) were established adjacent to the west coast of the US: Channel Islands (CI), Monterey Bay (MB), Gulf of the Farallones (GF), and Cordell Bank (CB) sanctuaries located in California, and Olympic Coast (OC) sanctuary in Washington (Fig. 1). The five sanctuaries cover 33,000 km² or approximately 4% of the west coast US EEZ off California, Oregon, and Washington. The US National Oceanic and Atmospheric Administration (NOAA) under the US Department of Commerce manages oversight of the sanctuaries and is responsible for protecting natural resources and facilitating multiple human uses within their boundaries. Although NOAA Fisheries and the Pacific Fishery Management Council manage specific fisheries in federal waters (3–200 NM offshore), the NOAA Office of National Marine Sanctuaries does not play a management role, but instead promotes its mandate to protect sanctuary ecosystems by retaining the authority to "manage human uses that may affect sanctuary resources" (NOAA-CBNMS, 2008). Because sanctuary managers and other conservation groups embrace an ecosystem-based approach that requires understanding marine ecology within the larger context of the CCLME, a guiding interest exists to acquire new information that will help determine the degree to which the CCLME, and specifically, the five sanctuaries function

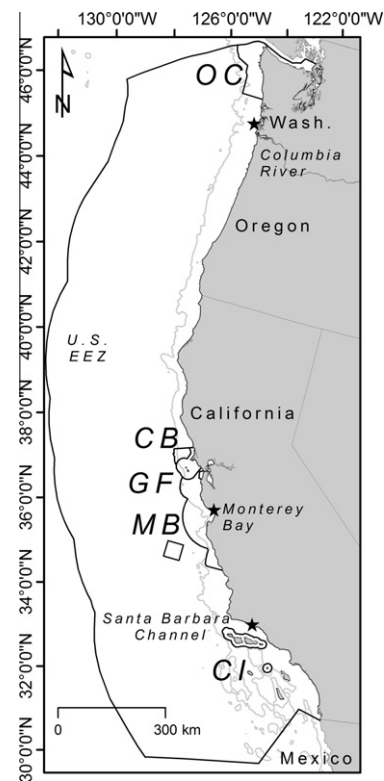


Fig. 1. US Exclusive Economic Zone including the five west coast National Marine Sanctuaries: Olympic Coast (OC), Cordell Bank (CB), Gulf of the Farallones (GF), Monterey Bay (MB), and Channel Islands (CI). Black stars indicate approximate locations where sooty shearwaters were captured for telemetry. The 1000-m isobath delineating the continental slope is indicated by the gray line.

as a network of interconnected habitats for mobile predators (i.e., seabirds and marine mammals) and important prey resources.

In the CCLME, important mesotrophic predators including sooty shearwater, common murre (*Uria aalge*), humpback whale (*Megaptera novaeangliae*), California sea lion (*Zalophus californianus*), salmon (*Oncorhynchus spp.*), and Pacific hake (*Merluccius productus*) depend on abundant prey species including, euphausiids (primarily *Thysanoessa spinifera* and *Euphausia pacifica*), market squid (*Loligo opalescens*), northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax caerulea*), Pacific herring (*Clupea harengus pallasi*), and juvenile rockfishes (*Sebastes spp.*; Field et al., 2006). Together, these key forage species are responsible for a great proportion of the total energy transferred to the region's abundant predators (Field et al., 2006). Commercial fisheries also target forage fishes in the CCLME. Off California, the majority of fishery landings in biomass, volume, and revenue include three forage species (anchovy, sardine, and squid; CDFG, 2003). The shearwater's consumption of these prey species is equivalent to 40–116% of the annual biomass of anchovy landed in California ports (see Weins and Scott, 1975; Krasnow, 1978; Chu, 1984; CDFG, 2003).

Because commercial fisheries and marine predators rely on food webs influenced by local and remote dynamic oceanographic processes (Mantua et al., 1997), effective management requires an overarching approach that includes addressing spatially-explicit habitats of ecological importance. To understand and manage these habitats requires an integration of species' natural histories, oceanography, and conservation principles (e.g., Hyrenbach et al., 2000; Thrush and Dayton, 2010). Herein, we used satellite telemetry to quantify the degree to which individual sooty shearwaters shared space with each other and how individuals distributed throughout the CCLME during the boreal summer. We contend that

these analyses together will shed light on the location of important “habitat hotspots” within and beyond sanctuary waters of the CCLME (see Palacios et al., 2006). Specifically, we hypothesize that shearwaters would respond to environmental variability during the summer and display interannual variability in their overall distribution within the CCLME. Given the species’ propensity for extreme aggregation at sea and observations of mass-movements of shearwaters along the coast, we expected tracked individuals would display similarity among range-wide utilization distributions. Furthermore, we expected that shearwaters would seek out discrete habitat hotspot areas within the CCLME and that overall time-spent among sanctuaries and non-sanctuary areas of the EEZ would be non-random (i.e., some sanctuaries would be occupied disproportionately with respect to their availability to free-ranging shearwaters).

2. Materials and methods

2.1. Shearwater telemetry

We captured shearwaters at night using a handheld spotlight and dipnet (Ronconi et al., 2010) from a 5-m Boston Whaler (Monterey Bay and Santa Barbara Channel) or 4-m Zodiac inflatable skiff deployed from NOAA R/V *Magister* at sea off the Columbia River, Washington (Fig. 1). After capturing ~4 to 7 birds (typically from rafting aggregations at sea) we transported them in plastic, folding pet carriers (460 × 250 × 350 mm; Shandong Zhongcai Packing Co., Ltd.) lined with cotton towels either to shore or to the R/V *Magister* for measurements, banding, and satellite transmitter attachments (Telonics® TAV-2630 platform terminal transmitters [PTTs]; 29 g or 3.5% body-mass-equivalent of mean shearwater mass [831 ± 7 g]). We attached PTTs to individuals’ mid-dorsum using a suture-tape-glue combination (MacLeod et al., 2008) and programmed PTTs to transmit every 60 s from late morning through early evening (1100–2100 PST). We chose this duty cycle to maximize daily regional satellite availability, the number of transmissions (i.e., total tracking period), and to encompass both diurnal movements and the important evening crepuscular foraging period when shearwaters often aggregate in large foraging flocks (thousands of individuals; J. Adams and H. Nevins pers. obs.) and exhibit clusters of dive activity around sunset (Shaffer et al., 2009). Because we could not recapture birds at sea, we attempted to match the estimated PTT battery life (90 days) based on duty cycle with our anticipated attachment duration (ca. 90 days) at which point we expected tags would become dislodged. We released birds at sea near their capture location or in the vicinity of other rafting shearwaters.

2.2. ARGOS data filtering and interpolation

We determined the geographic locations of individual birds using ARGOS (CLS America, 2011) and archived data via the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005). We used STAT to flag and manually correct “mirror” locations and we removed duplicate records (i.e., when ARGOS returned two records with same time), retaining the record with the more accurate location class (LC) or greater number of satellite messages. We filtered ARGOS data (LC-3 through LC-B) using a speed-distance-angle (SDA) filter (modified *sdafilter* function in the *argosfilter* package in R; Freitas et al., 2008). We specified a 16.7 m s⁻¹ speed threshold and used default settings for distances and angles (Freitas et al., 2008). Our speed threshold is slightly greater than the mean + 1 SE allometric prediction for flight speed over ground (15.9 m s⁻¹) among diving shearwaters flying with a 5 m s⁻¹ tailwind (see Table 2 in Spear and Ainley, 1997). To

estimate time spent per three bathymetric zones (ETOP02v2, 2006): shelf (0–200 m), slope (201–1000 m), and rise (>1000 m), and among sanctuary and non-sanctuary waters of the EEZ, we used the SDA-filtered data and generated hourly locations for consecutive locations separated by <8 h according to the linear interpolation method in Tremblay et al. (2006).

2.3. Brownian bridge utilization distributions

To estimate shearwater area use, we calculated 95% Brownian bridge utilization distributions (95UDs; Horne et al., 2007) for individuals in 2008 and 2009. We used the SDA-filtered location data to create individual 95UD raster layers (3 × 3 km pixel) in R (function *kernelbb*, *adehabitat* package; Calenge, 2006). We selected only the shearwater tracking data within the CCLME (defined here as a rectangle bounded by 26–54° N latitude, 130° W longitude, and the western coastline of North America; Fig. 2). To create 95UDs, we specified the first (16.7 m) and second (3 km) smoothing parameters which relate to shearwater speed and ARGOS location estimate inaccuracy, respectively. Because the Brownian bridge movement model assumes a circular normal error distribution, the second smoothing parameter (3 km) approximates the circular standard deviation estimated from the median circular error probable (defined here as the individually averaged, 68th percentile ARGOS LC-specific locational errors from SDA-filtered data; see Costa et al., 2010). These parameters yielded appropriate estimates of space-use at the scale of the ARGOS data and for the purposes of this study. We mapped raster layers in ArcMap 9.3.1 (ESRI, Redlands, CA) using the USA contiguous Albers equal area conic (USGS version) projection based on WGS 84 geoid data.

We defined “habitat hotspots” as those areas where the probabilities of locating the tagged group of shearwaters were greatest and where multiple individuals co-occurred in space. Specifically, to identify hotspots during each year, we first summed the individual 95UD raster values (Σ_n 95UD). We then weighted each 3 × 3 km Σ_n 95UD pixel according to the number of unique shearwaters therein, using the formula:

$$95UD\ DWI = \Sigma_n 95UD / n_t^{-1}, \quad (1)$$

where n_t was the number of unique individual 95UD surfaces overlapping the pixel. Thus, 95UD DWI estimates for pixels occupied by fewer shearwaters were down-weighted relative to those occupied by a greater number of shearwaters (see MacLeod et al., 2008). We consider the fourth quartile values of 95UD DWI to represent shearwater hotspots and third quartile values to represent important areas. This down weighting and quartile approach is similar to hotspot definitions derived for single-species based on ship transect density data at sea (Nur et al., 2011), however in our case, 95UD DWI replaces species-specific density at sea.

To assess similarity in space-use sharing among individuals within years (proportion of animal i ’s 95UD volume that overlapped with animal j ’s 95UD volume), we calculated the volume of intersection (VI) statistic in R (function *kerneloverlap*, *adehabitat* package; Calenge, 2006; see Eq. (5) in Fieberg and Kochanny, 2005). The VI provides a singular measure of the similarity between two UD estimates and can be used conditionally on partial UDs. Because we calculated VI using the 95UDs, we scaled VI to range between 0 (no space-use sharing) to 1 (identical space-use). For each individual, we estimated mean VI with all other individuals within each year. We compared mean VI between years and among capture locations using a 2-way analysis of variance (ANOVA) after arcsine square root transformation to ensure normality of proportional data.

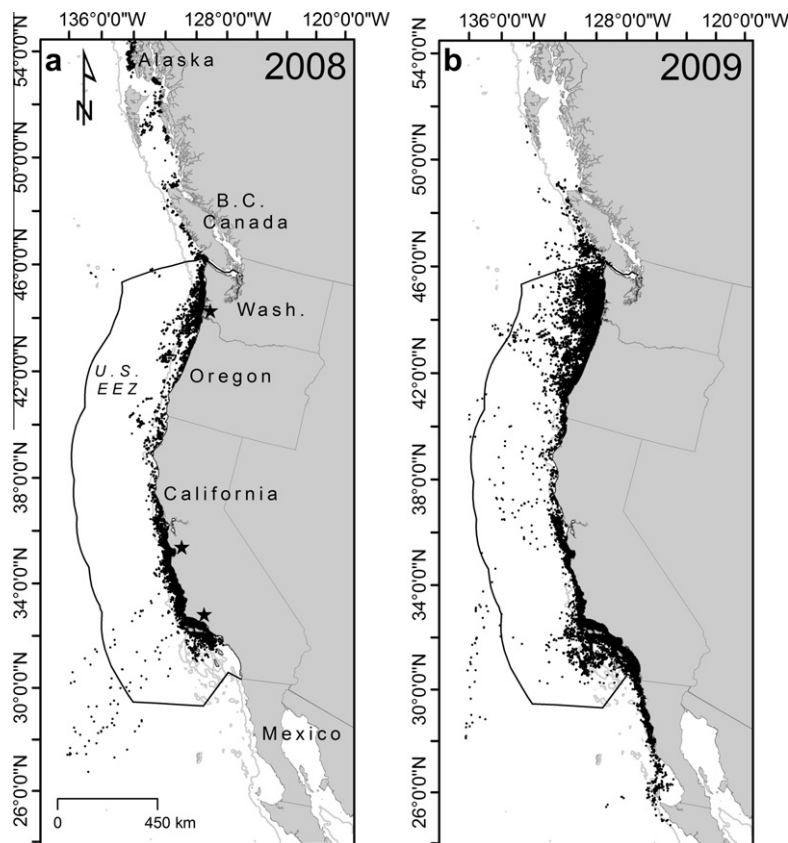


Fig. 2. The California Current Large Marine Ecosystem (CCLME) study area showing the US EEZ boundary and the sub-set of SDA-filtered sooty shearwater locations during 2008 (a) and 2009 (b) used in utilization distribution analyses. Black stars indicate approximate shearwater capture locations and the 1000-m isobaths are shown by the gray line.

2.4. Shearwater use of national marine sanctuaries: compositional analyses

We estimated the proportions of the individual 95UD volumes within the west coast EEZ (excluding Alaska), and all five west coast sanctuaries. We then used compositional analysis (Aebischer et al., 1993) to determine if 95UD volumes (i.e., ‘used areas’) were distributed proportionately with respect to the EEZ and sanctuary zones. To do this, we identified the area of each zone potentially available (i.e., ‘available area’) for the set of shearwaters. We assumed that the available area for the set of shearwaters in each year was consistent and included all ocean waters bounded by our delineation of the CCLME (i.e., 26–54° N latitude and 130° W longitude, which enclosed the greatest latitudinal extent of tracked shearwaters). We then calculated the proportion of each shearwater’s 95UD volume that intersected with each zone. To determine whether shearwaters were distributed disproportionately within one zone versus another, we compared the relative proportion of the ‘available areas’ within each zone to the relative proportions of the 95UD volumes within each zone. For compositional analysis we used the randomization test in R (function *compana*, adehabitat package; Calenge, 2006). All other parameters (e.g., the number of replicates, zero replacement values, and alpha thresholds) were set using default values.

3. Results

We recorded daily movements among 57 sooty shearwaters (11 ± 0.2 SE locations per duty cycle d^{-1}) between June–October in 2008 ($n = 28$ shearwaters; $n = 24,077$ SDA-filtered locations;

tracking duration: 96 ± 3 d SE; Fig. 2a) and 2009 ($n = 29$; $n = 34,862$ SDA-filtered locations tracking duration: 121 ± 5 d SE; Fig. 2b, Appendix A). In 2008 and 2009, we deployed PTTs on shearwaters in Monterey Bay (MB; 2008: $n = 12$; 2009: $n = 13$), Santa Barbara Channel (SBC; 2008: $n = 9$; 2009: $n = 11$), and off the Columbia River Plume (CRP; 2008: $n = 7$; 2009: $n = 5$; Appendix A, Fig. 1). In 2009, four individuals remained within the CCLME into November and two individuals remained into December. Shearwaters ranged throughout the entire length of the CCLME, from south-east Alaska through mid-Baja California, Mexico (Fig. 2). Although shearwaters were distributed farther from shore and farther to the south in 2009, in both years they mostly utilized shelf waters (<200-m depth): 68% of total time during 2008 and 46% of total time during 2009. However, they also spent considerable time over the continental slope (201–1000-m depth) in both years: 27% of total time during 2008 and 43% of total time during 2009. Shearwaters rarely occupied waters beyond the continental slope (>1000-m depth) during 2008 and 2009: 5% and 12% of total time, respectively).

3.1. Sooty shearwater utilization among west coast sanctuaries within the US EEZ

Within the west coast US EEZ, shearwaters displayed variability in sanctuary use (Appendix A, Fig. 3). During 2008, shearwaters spent only $22 \pm 2\%$ of their time within the five sanctuaries. In 2008, shearwaters captured at the CRP visited all but the CI sanctuary (2 of 7 shearwaters spent >25% of their time within sanctuaries); shearwaters captured in MB visited all but the CB sanctuary (6 of 12 shearwaters spent >25% of their time within

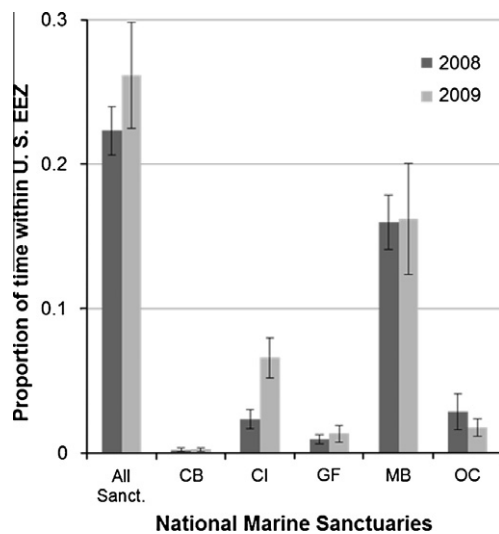


Fig. 3. Mean proportion (± 1 SE) of individual shearwaters' time within the US EEZ during 2008 and 2009 spent within the five west coast US National Marine Sanctuaries: Cordell Bank (CB), Channel Islands (CI), Gulf of the Farallones (GF), Monterey Bay (MB), and Olympic Coast (OC). Also shown is proportion of total time within all NMS combined.

sanctuaries); shearwaters captured in the SBC visited all sanctuaries (2 of 9 spent >25% of their time within sanctuaries; Appendix A). In 2009, overall total time spent within sanctuaries was similar to 2008 ($25 \pm 4\%$; Appendix A, Fig. 3). In 2009, one of 5 shearwaters captured at the CRP visited all five sanctuaries (19% of its total time); shearwaters captured in MB visited all sanctuaries (9 of 13 spent >25% of their time within sanctuaries with 8 of these 9 spending >25% within the MB sanctuary); shearwaters captured in the SBC visited all five sanctuaries; 1 of 11 spent >25% of its time within sanctuaries (Appendix A).

In both years and among all five sanctuaries, shearwaters spent greatest amount of time within the MB sanctuary (ca. 16% of total time within the EEZ) and least amount of time within the CB and GF sanctuaries (<1% of total time within the EEZ; Appendix A, Fig. 3). In 2008, shearwaters utilized the MB sanctuary and non-sanctuary waters of the west coast US EEZ in greater proportions relative to the availability of these zones within the CCLME (compositional analyses, Wilkes Lambda = 0.167, $P = 0.002$; Table 1). The MB sanctuary ranked highest according to utilization vs. available area, followed by the EEZ outside sanctuary waters. Weak differences among the remaining sanctuaries precluded meaningful ranking. In 2009, shearwaters again utilized the available zones disproportionately (Wilkes Lambda = 0.325, $P = 0.002$; Table 2) and were more likely to utilize the CI and MB sanctuaries and EEZ waters outside sanctuaries.

Table 1

Proportional area-use of non-Sanctuary US Exclusive Economic Zone (EEZ) waters and waters within five west coast National Marine Sanctuaries: Cordell Bank (CB), Channel Islands (CI), Gulf of the Farallones (GF), Monterey Bay (MB), and Olympic Coast (OC) by satellite-tracked sooty shearwaters in 2008 and 2009. Tabulated parameters include percentage of total available area represented by each zone, percentage of individuals' 95UD volumes that overlap each zone, and the ranking of each zone (1–6, greatest to least use, respectively) according to compositional analysis used to test whether, relative to the total available area, the individual shearwaters' 95UDs overlapped disproportionately with specific zones.

	Zone					
	Non-sanctuary EEZ	CB	CI	GF	MB	OC
Percentage of total available area	96.04	0.17	0.45	0.41	1.93	1.00
2008 ($n = 28$)						
Percentage of individuals' 95UDs overlapping each zone (mean \pm SE)	78.26 \pm 4.07	0.24 \pm 0.31	2.65 \pm 1.79	0.80 \pm 0.66	15.71 \pm 4.39	2.33 \pm 2.19
Rank (Compositional Analysis; Wilkes Lambda = 0.167, $p = 0.002$)	2	5	3	4	1	6
2009 ($n = 29$)						
Percentage of individuals' 95UDs overlapping each zone (mean \pm SE)	72.72 \pm 9.80	0.15 \pm 0.21	6.74 \pm 3.32	1.20 \pm 1.42	17.66 \pm 10.18	1.53 \pm 1.22
Rank (Compositional Analysis; Wilkes Lambda = 0.325, $p = 0.002$)	3	5	1	4	2	6

3.2. Space-use sharing among individual shearwaters

Overall, individual shearwater UD were more similar in 2008 ($VI = 0.35 \pm 0.02$ SE) than in 2009 ($VI = 0.14 \pm 0.01$ SE; two-way ANOVA, $F_{1,51} = 52.40$, $p < 0.0001$). Similarity also differed among capture location (two-way ANOVA, $F_{2,51} = 13.49$, $p < 0.0001$; non-significant year \times location interaction, $p = 0.707$); in 2008, similarity among shearwaters captured at the same location ranged from 0.16 (CRP) to 0.48 (MB; Table 2) and in 2008, mean similarity among shearwaters from different capture location groups ranged from 0.22 (SBC cf. CRP) to 0.42 (SBC cf. MB; Table 2). In 2009, mean similarity among shearwaters within the same capture location group was less and ranged from 0.19 (CRP) to 0.25 (MB; Table 2) and similarity among shearwaters from different capture locations in 2009 also was less than in 2008, ranging from 0.04 (CRP cf. MB) to 0.13 (SBC cf. MB; Table 2).

3.3. Sooty shearwater hotspots in the CCLME

Patterns in shearwater 95UD DWI during 2008 and 2009 revealed variability in the location and spatial extent of hotspots throughout the CCLME (Figs. 4 and 5). In 2008, shearwaters in the northern CCLME region mostly were confined to the inner shelf (<200 m depth) between Heceta Bank, Oregon and the OC sanctuary (Fig. 4a). Relatively important areas (2nd quartile values) occurred north of the Columbia River off Willapa Bay and Grays Harbor, Washington, but did not extend into the OC sanctuary. In the central CCLME region, shearwaters in 2008 largely occupied continental shelf and shelfbreak waters (Fig. 4a). Hotspots (4th quartile values) included the central, inshore Monterey Bay Canyon, but a significant aggregation representing 68–89% of tracked shearwaters from all three capture sites, occupied the inner shelf area from Estero/San Luis Obispo Bay to Point Arguello (region to the north of Point Conception; Fig. 4c). South of Point Conception, California, shearwaters in 2008 primarily occurred within basin (>200-m depth) waters of the north-central SBC (Fig. 4b).

Shearwater distribution in 2009 was appreciably different from 2008. The total extent of shearwater 95UDs in 2009 ($39,105 \text{ km}^{-2}$; Fig. 5a) was four-times greater than in 2008 (9000 km^{-2} ; Fig. 4a). In 2009, overall dispersion was greater and extended westward farther offshore beyond the continental shelf-rise (>2000 m depth; Figs. 1b and 5a). Shearwaters again aggregated close to shore (within 50 km) and discrete hotspots (4th quartile values) were associated with the Willapa Bay/Grays Harbor area from the Columbia River to the southern border of the OC sanctuary (Fig. 5a and b). Within the northern region, two additional important areas occurred in 2009 in Oregon: inshore from Heceta Bank (3rd quartile values) and along the shelfbreak off Cape Blanco (3rd and 4th quartile values; Fig. 5b). In 2009, shearwaters in the central region occupied a narrower band centered over the inner

Table 2

Annual comparisons of the mean (\pm SE) index of volume intersection (VI; a measure of space-use similarity) based on individual sooty shearwater 95UDs and according to capture location: Columbia River Plume (CRP), Monterey Bay (MB), and Santa Barbara Channel (SBC).

	CRP	MB	SBC
2008			
CRP	0.15 \pm 0.04	0.25 \pm 0.02	0.21 \pm 0.03
MB		0.45 \pm 0.01	0.40 \pm 0.01
SBC			0.38 \pm 0.03
2009			
CRP	0.18 \pm 0.04	0.04 \pm 0.01	0.05 \pm 0.01
MB		0.24 \pm 0.02	0.12 \pm 0.01
SBC			0.20 \pm 0.01

continental shelf. Because shearwaters in 2009 were more widespread and less aggregated, total hotspot areas were greater in area (e.g., the entire Monterey Bay; Fig. 5d). Aggregative distribution within the GF sanctuary (3rd quartile values) was closely aligned with the shelfbreak and this ridge-like pattern in UD extended south from the GF sanctuary through the northern MB sanctuary and into Monterey Bay. Hotspots in the southern central areas (e.g., Estero/San Luis Obispo Bay) were slightly more isolated and closer to shore (Fig. 5d). In 2009, shearwaters occupied a large proportion of the Southern California Bight and especially waters within ca. 40 km of the coast from the southeastern SBC south to the California-Mexico border (Fig. 5d and e). Two additional small

(153 km² total area) hotspots (4th quartile values) occurred near the California-Mexico border and off Cabo Colnett, Baja California, Mexico.

4. Discussion

4.1. Similarity in space-use among individual shearwaters

Volume of intersection (VI) analysis indicated that shearwaters captured at three widely separated areas (hundreds to thousands of km apart) shared similar utilization distributions (e.g., VI = 0.35 among all birds in 2008). Such a large measure similarity of space-use at the scale of the CCLME is testament to the aggregative nature of the region's shearwater population. Although birds from all three capture sites overlapped, there was less similarity in space-use in 2008 and 2009 among birds captured at the CRP and those captured in MB and the SBC. It is possible that when productivity and prey availability remains high off Washington (or prey composition changes or availability becomes decreased to the south), the CRP may indeed represent a discrete wintering area for some proportion of migrating shearwaters. Shearwaters captured at all three sites utilized waters associated with the CRP, especially in 2009, when birds captured in June tended to remain in this area through September when they were joined by several individuals captured off MB and the SBC. Lesser use of the CRP area in 2008 resulted from a rapid dispersal event among CRP shearwaters in July (approximately 3 weeks after capture) that coincided

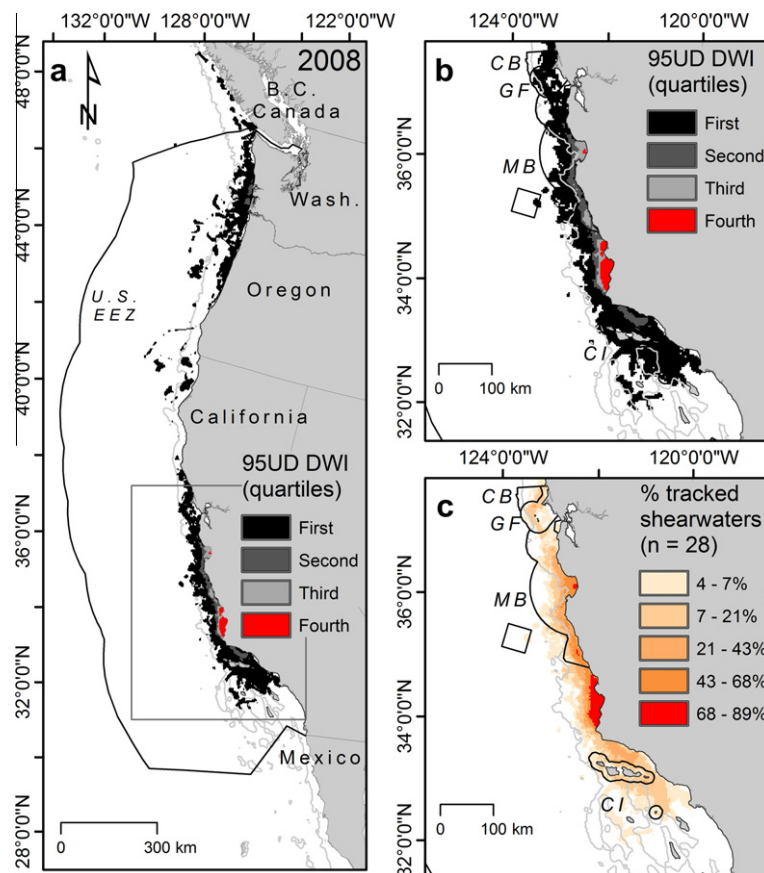


Fig. 4. Sooty shearwater 95% utilization distribution down-weighted index (95UD DWI; see text) displayed by quartiles, with the fourth quartile (red) indicating shearwater 'habitat hotspot' areas in 2008. (a) Gray box indicates central – southern California focal area expanded in sub-panels b and c. Sub-panel (b) shows 95UD DWI associated with sanctuaries within the US EEZ including, Cordell Bank (CB), Gulf of the Farallones (GF), Monterey Bay (MB), and Channel Islands (CI). Sub-panel (c) shows the percent of total number of individual shearwaters' 95 UD within each 3 × 3 km pixel for the 2008 summed UD used to calculate the 95 UD DWI. 1000-m isobath is indicated by the light-gray line.

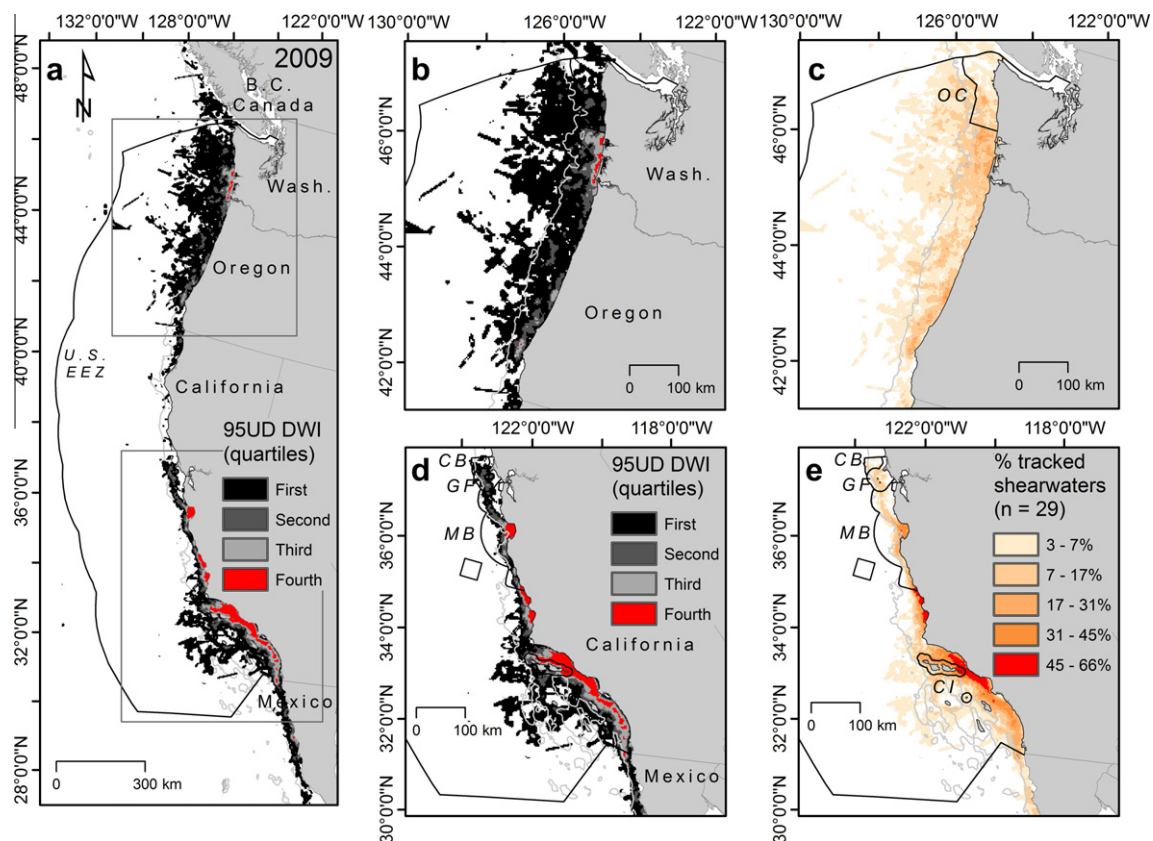


Fig. 5. Sooty shearwater 95% utilization distribution down-weighted index (95UD DWI; see text) displayed by quartiles, with the fourth quartile (red) indicating shearwater 'habitat hotspot' areas in 2009 (a). Gray boxes indicates Oregon-Washington focal area expanded in sub-panels b and c and central – southern California focal area expanded in d and e. Sub-panel data as in Fig. 4b and c showing sanctuaries within the US EEZ including, Olympic Coast (OC), Cordell Bank (CB), Gulf of the Farallones (GF), Monterey Bay (MB), and Channel Islands (CI).

with the onset of a prolonged upwelling event that affected the northern CCS (Nakagawa et al., unpublished data). Lesser VI indices in 2009, both within and among capture site groupings coupled with the four-fold increase in total area occupied by the tracked shearwaters indicate that individuals in 2009 spent more time transiting or searching, perhaps because food either was more difficult to locate, more patchily distributed, or of a different type (i.e., differing interannual availability of krill vs. squid vs. forage fishes).

4.2. Sooty shearwater distribution in the CCLME: defining regional hotspots

Movements of individual sooty shearwaters contribute a new look at their distribution within the CCLME and provide unique insight to regionally discrete shearwater "hotspots" and areas of relative importance (i.e., the upper fourth and third quartiles in the annual 95UD DWIs, respectively). For example, we found considerable interannual variability in distribution and aggregation patterns. The more pronounced CRP area hotspot in 2009, compared with 2008, is consistent with greater densities and overall numbers of sooty shearwaters observed there during fisheries surveys in May and June 2009 compared with 2008 (Zamon et al., unpublished data). This region is strongly influenced by the Columbia River, which forms a characteristic plume of fresh, nutrient-enriched water that mixes and flows northward to Willapa Bay and Grays Harbor, WA, especially during weak upwelling events or transitions to downwelling conditions (Horner-Devine, 2009). Annual (since 1998) fisheries surveys conducted by NOAA Fisheries have demonstrated that this area supports a large biomass of

important forage fishes including northern anchovy, juvenile salmonids, Pacific herring, and whitebait smelt (*Allosmerus elongates*; Emmett et al., 2006); this area also is a persistent seabird hotspot in the spring-summer, especially for shearwaters and common murre (J. Zamon et al., unpublished data). Kudela et al. (2010) suggested that the CRP plume provides a biological refuge area, or "bioreactor effect", where trophic transfer is enhanced by fluvial inputs—especially during periods of weak to no upwelling—as might occur during El Niño events. The plume in general supports large numbers of juvenile salmonids (De Robertis et al., 2005) and northern anchovy (Richardson, 1981). It is interesting to note that although shearwaters in this study used the OC sanctuary, just to the north of the CRP, the OC sanctuary did not appear to support hotspot areas for tracked shearwaters in either year (Figs. 4 and 5). This is in contrast with the findings by Nur et al. (2011) which indicated that the OC sanctuary ranks higher than the CRP according to three hotspot criterion calculated by using vessel transect data.

Off central to southern Oregon in 2009, a region with no sanctuaries and very little marine protected area, we observed relatively important shearwater areas (3rd quartile in 95UD DWI, Fig. 5b) near Heceta Bank and Cape Blanco. Both areas are well known for supporting greater relative densities of seabirds. Briggs et al. (1992) documented large numbers of shearwaters and greatest densities in these two areas. Ainley et al. (2005) suggested that this area could act as a productive refuge when the CCLME experiences periodic decreased productivity. For instance, during May 2000, they estimated ~475,000 shearwaters occurred off central to southern Oregon (decreasing to ~63,000 in August 2000); this

however, only equates to perhaps <10% of the total number of shearwaters in the CCLME during peak abundance. In our study, greatest shearwater utilization occurred inshore from Heceta Bank compared with distribution reported by Ainley et al. (2005), but distribution to the north of Cape Blanco was similar. Such interannual variability in the cross-shelf distribution of 'dark' shearwaters (vast majority in the CCLME are sooty shearwaters) was observed off the Strait of Juan de Fuca by Yen et al. (2005) and off central California by Oedekoven et al. (2001), and was attributed to oceanographic variability. Although these two areas likely are important for shearwaters at a local scale (Ainley et al., 2005), in this study they were not utilized nearly as much as the CRP or continental shelf waters off southern central California in 2008 and 2009.

Off central California, local-scale patterns revealed by our telemetry are consistent with previous density distributions measured at sea (Briggs et al., 1983; Briggs and Chu, 1986; Oedekoven et al., 2001). For example, Briggs et al. (1983) reported that shearwaters did not frequent to a great degree California waters north of the CB sanctuary. Additionally, off Central CA, Oedekoven et al. (2001) found shearwaters were closely aligned with the shelfbreak, with a trend toward more inshore distribution during the early 1990s. Consistent with our telemetry, Monterey Bay previously has been identified as an important area for sooty shearwaters (Briggs et al., 1987; Briggs and Chu, 1986; Ford et al., 2004). This region is well known for supporting large concentrations of forage fishes and euphausiids (Marinovic et al., 2002; Croll et al., 2005) and commercial harbors here support an active purse-seine fishing fleet that targets anchovy, sardine, and squid. Somewhat unique, our data indicate that the Estero/San Luis Obispo Bay area, outside the MB sanctuary and a poorly surveyed area (but see Mason et al., 2007), is important and can support large numbers of foraging shearwaters for weeks to months (i.e., 68–89% of the tracked population in 2008; Fig. 4c). Currently, there is relatively little commercial forage fish take in this area.

Waters of the Southern California Bight were well utilized by tracked shearwaters, especially during 2009. The 95UD DWI indicated a contiguous area of importance that extended through the southeast SBC waters to the US–Mexico border. Our observations are consistent with previous vessel survey data that indicate greatest spring–summer concentrations in the vicinity of the northern Channel Islands (Mason et al., 2007) and downstream from the upwelling cell centered at Point Conception (Briggs et al., 1987; Yen et al., 2006). The strong, seasonal thermal front that crosses the SBC (Breaker et al., 2003) appears to be the principle feature delineating the westward-extent of the concentration of shearwaters and spawning biomass of sardine and anchovy which occur mostly on the warmer side (~12–15 °C). Shearwater distribution also may be affected by regionally persistent circulation features (e.g., cyclonic eddies) in the SBC (Oey et al., 2001) which have been shown to aggregate larval–juvenile fishes near the surface (Nishimoto and Washburn, 2002); such features have been suggested as important for shearwaters (Yen et al., 2006) and other seabirds (Adams et al., 2010).

Ford et al. (2004) showed that for the Central California region, greatest biomass of seabirds at sea (dominated by sooty shearwaters) occurred closer to shore, yet seabird community diversity was greatest farther offshore near the shelfbreak. Unraveling such single-species and community-level patterns in the future would be important for considering spatial planning targeting regions that support areas of maximum energy transfer to only a few species (e.g., shearwaters in the CCLME) vs. those with high species diversity (cf. Nur et al., 2011). Although it would be desirable to have appropriate environmental proxies to better predict species distributions at sea at a regional scale, more effort is required to deter-

mine which variables can be used to enhance predictive species distributions (Yen et al., 2004a,b; Louzao et al., 2006).

4.3. Can shearwater telemetry inform marine spatial planning?

Previously, it has been difficult to understand how the spring–summer shearwater population is distributed through time regionally (and especially locally) within the CCLME (Briggs and Chu, 1986). Satellite telemetry provides for greater continuous time-scales to evaluate seasonal, non-restricted at-sea distributions. Our results bridge nested-scales of analyses (cf. basin-wide wintering areas described in Shaffer et al., 2006) and provide a greater understanding of the population dispersion and ranging patterns within the CCLME, including a first look at regional, fine-scale movements amongst multiple hotspot areas and use of the west coast National Marine Sanctuaries.

Future marine spatial planning will benefit from an increasing understanding of the distribution of similar abundant mesopredators and their habitat affinities. Our results indicate persistent use by shearwaters of upwelling shadows (Graham and Largier, 1997) and coastal embayments such as northern Monterey Bay, Estero/San Luis Obispo Bays, and the Santa Barbara Channel in California. These upwelling retention areas display unique watermass properties (e.g., temperature and color), form in predictable locations along the west coast downstream from upwelling centers where wind-forced offshore Ekman transport is reduced by a marked change in the coastline orientation from northwest-southeast to west-east trending. In fact, along with enhanced primary productivity associated with the CRP, Monterey Bay, and Estero/San Luis Obispo Bays, also offer additional important spatial refuges or 'oases' for abundant, mobile mesopredators during periods of reduced upwelling or during periods of reduced productivity (e.g., during El Niño events; Marinovic et al., 2002; Benson et al., 2002). Although these habitats are well known to support large populations and aggregations of forage species and mesopredators alike, and portions are currently enclosed by sanctuary boundaries—forage fish remain a lucrative target for commercial fisheries (CDFG, 2001). The distribution of sooty shearwaters in this study highlights the importance of regions outside sanctuaries that tend to be farther from commercial fish landing facilities. These areas may become increasingly important to abundant mesopredators in the future given high global harvests and potential for expanding forage fish fisheries (Alder et al., 2008), recovery of large rorquals (see Ainley and Hyrenbach, 2010), and changing upwelling dynamics associated with climate change (Snyder et al., 2003). Additional priority conservation areas outside sanctuaries may be warranted in the future, especially if expected changes within the CCLME cause abundant predators and fisheries to share limited, overlapping resources (see Pichegru et al., this issue).

The CCLME embodies great ecological complexities, and sorting out environmental–climatological variability (e.g., ENSO, PDO, timing and strength of upwelling), anthropogenic impacts (e.g., ongoing industrial fisheries and historic whaling), and interspecific interactions (e.g., interference competition) should be considered when implementing ecosystem-based management and marine spatial planning (Thrush and Dayton, 2010). Although a complete understanding of 'normal' patterns in species distributions and interactions will certainly be overshadowed by "shifting baselines" characteristic of altered marine ecosystems (c.f., Jackson, 2008; Pauley, 2005). To this end, we contend that timely and effective implementation of effective spatial conservation will require additional studies of biological indicator species of certain foraging-guilds within marine ecosystems. Pragmatically, while consideration of appropriate areas for conservation will vary based on species-specific abundances, community-wide diversity patterns, and

habitat requirements for diverse foraging guilds—focusing on numerically dominant species representative of distinct foraging guilds is a logical starting point (see Devictor et al., 2007). One possibility would be to enact spatial closures or spatially-explicit protections based on environmental conditions readily measurable from remote sensing, or driven by the timing of seasonal events (i.e., pre-migration staging areas) or environmentally-driven triggers (i.e., ENSO/PDO index) that might precipitate an incursion of species into forecast management areas or may lead to redistribution or increased, yet predictable, spatial aggregation (as occurred in 2008 when CCLME-wide shearwaters converged on Estero/San Luis Obispo Bays; Fig. 4; see also Hyrenbach et al., 2000; Hooker et al., 2011). Given the sooty shearwater's great abundance and its association with productive marine habitats overlying the northeastern Pacific continental shelf-slope domain, we contend that this seabird species is an appropriate indicator of important forage fish habitats and can assist marine spatial planning approaches in the CCLME. Methods and results herein add to a growing number of studies that will be used to inform managers charged with the design and management of spatially-explicit conservation actions, involving implementation and evaluation of Marine protected Areas [MPAs] or new Important Bird Areas [IBAs], within the incipient marine spatial planning paradigm. Of next most importance to better understanding shearwater distributions at sea, is the need to evaluate differences in patterns derived using vessel observations at sea with distribution measured using telemetry (see Nur et al., 2011 and Camphuysen et al., this issue) and patterns associated with environmental variables.

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Appendix A

Summary of 2008 and 2009 non-breeding season sooty shearwater satellite telemetry within the CCLME, including: Capture location Columbia River Plume, WA (CRP); Monterey Bay, CA (MB); and, Santa Barbara Channel, CA (SBC), Bird ID, start and end dates, tracking duration (days), latitudinal extent, and proportion of time within the US Exclusive Economic Zone (EEZ) spent within the five west coast National Marine Sanctuaries: Cordell Bank (CB), Channel Islands (CI), Gulf of the Farallones (GF), Monterey Bay (MB), and Olympic Coast (OC).

Bird	Start Date	End Date	Duration (days)	Latitude extent (degrees)		Proportion of time within US EEZ by 2sanctuary zone					
				South	North	Total NMS	CB	CI	GF	MB	OC
CRP 209	6/19/08	10/8/08	112	31.0	47.3	0.12	–	–	<0.01	0.10	0.02
210	6/20/08	9/15/08	87	46.3	55.0	0.18	–	–	–	–	0.18
211	6/20/08	10/9/08	112	27.7	46.4	0.29	0.03	–	0.04	0.23	–
212	6/20/08	9/18/08	91	45.2	56.1	0.28	–	–	–	–	0.28
215	6/20/08	10/1/08	103	41.5	48.3	0.13	–	–	–	–	0.13
217	6/19/08	10/3/08	106	27.8	47.7	0.23	–	–	<0.01	0.21	0.02
218	6/19/08	10/10/08	113	27.3	46.7	0.19	0.01	–	0.06	0.11	–
MB 219	7/1/08	9/27/08	89	29.9	36.8	0.11	–	–	–	0.11	–
223	7/1/08	9/30/08	91	27.9	37.0	0.27	–	–	–	0.27	–
224	7/1/08	10/10/08	101	34.4	48.6	0.28	–	–	<0.01	0.20	0.07
229	7/2/08	10/5/08	95	33.7	39.2	0.32	–	–	–	0.32	–
230	7/4/08	10/9/08	97	28.7	46.2	0.17	–	–	<0.01	0.17	–
231	7/4/08	10/3/08	91	34.6	48.0	0.25	–	–	<0.01	0.17	0.07
232	7/2/08	9/26/08	86	34.6	47.2	0.26	–	–	0.01	0.25	<0.01
233	7/1/08	9/26/08	87	33.9	37.3	0.24	–	0.04	–	0.21	–

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Bird	Start Date	End Date	Duration (days)	Latitude extent (degrees)		Proportion of time within US EEZ by 2sanctuary zone					
				South	North	Total NMS	CB	CI	GF	MB	OC
234	7/4/08	9/13/08	71	34.4	37.0	0.11	–	–	–	0.11	–
235	7/2/08	9/19/08	80	34.0	44.4	0.33	–	0.04	0.01	0.27	–
237	7/2/08	8/19/08	48	33.8	37.2	0.42	–	0.11	–	0.32	–
238	7/2/08	9/29/08	89	32.8	36.8	0.05	–	–	–	0.05	–
SBC 213	6/27/08	10/7/08	103	30.6	37.2	0.25	–	0.03	–	0.22	–
214	6/27/08	10/9/08	104	33.1	38.8	0.41	0.02	–	0.04	0.35	–
216	6/27/08	10/5/08	100	30.7	41.5	0.18	<0.01	0.05	<0.01	0.13	–
220	6/28/08	10/13/08	107	33.1	48.5	0.15	–	0.04	0.03	0.06	0.02
221	6/28/08	10/26/08	120	32.9	40.9	0.27	<0.01	0.01	0.03	0.23	–
222	6/28/08	10/7/08	100	28.2	36.8	0.15	–	0.08	–	0.07	–
226	6/27/08	10/5/08	100	33.9	37.7	0.19	–	0.07	–	0.12	–
227	6/28/08	10/6/08	100	28.0	38.0	0.16	–	0.07	0.01	0.08	–
228	6/28/08	10/5/08	99	33.4	37.6	0.25	–	0.12	<0.01	0.13	–
2008 averages (± SE)			96 ± 3			0.22 ± 0.02	<0.01	0.02 ± 0.01	<0.01	0.16 ± 0.02	0.03 ± 0.01
CRP 556	5/16/09	9/5/09	112	41.0	51.1	0.09	–	–	–	–	0.09
557	6/7/09	10/2/09	117	40.4	48.9	0.09	–	–	–	–	0.09
558	6/7/09	12/2/09	178	31.4	51.2	0.13	–	–	–	–	0.13
559	6/7/09	6/28/09	21	40.2	47.1	–	–	–	–	–	–
560	6/7/09	11/26/09	172	32.8	49.0	0.19	<0.01	0.15	<0.01	0.01	0.02
MB 561	6/19/09	10/10/09	113	30.2	42.1	0.20	–	0.05	0.03	0.13	–
562	6/19/09	10/28/09	131	33.9	38.8	0.64	<0.01	<0.01	<0.01	0.63	–
563	6/19/09	10/22/09	125	28.9	37.9	0.36	<0.01	0.06	0.01	0.28	–
565	6/20/09	12/11/09	174	32.7	48.9	0.16	<0.01	0.06	<0.01	0.01	<0.01
566	6/20/09	10/27/09	129	29.2	45.1	0.15	<0.01	0.06	<0.01	0.08	–
567	6/20/09	10/16/09	118	34.1	46.1	0.57	–	<0.01	–	0.56	–
568	6/20/09	10/14/09	116	28.5	38.3	0.68	<0.01	–	0.15	0.53	–
569	6/27/09	10/22/09	117	29.0	38.2	0.52	0.03	0.08	0.08	0.34	–
570	6/27/09	11/5/09	131	32.4	52.7	0.24	<0.01	0.13	<0.01	0.06	0.04
571	6/27/09	10/29/09	124	34.4	49.0	0.51	<0.01	–	<0.01	0.49	0.02
572	6/27/09	10/25/09	120	34.6	47.8	0.54	–	–	<0.01	0.51	0.02
573	6/27/09	10/14/09	109	31.9	40.1	0.40	–	0.16	–	0.24	–
574	6/27/09	10/25/09	120	33.5	47.9	0.34	<0.01	–	<0.01	0.31	0.02
SBC 236	7/1/09	11/20/09	142	27.8	44.9	0.19	<0.01	0.11	0.01	0.08	–
575	6/30/09	10/13/09	105	32.4	41.5	0.09	<0.01	0.06	<0.01	0.02	–
576	6/30/09	10/24/09	116	33.0	48.6	0.12	–	0.07	–	0.04	0.01
577	7/1/09	10/9/09	100	27.0	36.9	0.01	–	<0.01	–	0.01	–
578	6/30/09	10/13/09	105	31.1	36.9	0.07	–	0.02	–	0.04	–
579	6/30/09	10/19/09	111	32.2	37.9	0.18	–	0.11	0.04	0.02	–
581	7/1/09	10/5/09	96	28.4	35.7	0.10	–	0.06	–	0.03	–
582	7/1/09	11/1/09	123	32.4	46.9	0.06	–	0.06	–	–	–
583	7/1/09	10/4/09	95	29.1	35.5	0.36	–	0.36	–	–	–
584	7/1/09	10/27/09	118	33.2	49.6	0.19	<0.01	0.10	–	0.03	0.05
585	7/1/09	12/7/09	159	32.3	47.9	0.15	<0.01	0.12	<0.01	0.02	0.01
2009 Averages (±SE)			121 ± 5			0.25 ± 0.04	<0.01	0.07 ± 0.01	0.01 ± 0.01	0.16 ± 0.04	0.02 ± 0.01

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